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# How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions?

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In the king penguin (*Aptenodytes patagonicus*), both pair members alternate in incubating and rearing their chick. Mates can recognize each other among thousands of other birds in the hubbub of the colony using only acoustic signalling—the display call. Large penguin colonies are found on sub-Antarctic islands where strong winds blow throughout the year. We have shown by experiments under natural conditions that the level of background noise increases in windy conditions and thus leads to a diminution of the signal-to-noise ratio. Moreover the emergence level of the signal revealed by entropy calculation is statistically weaker in windy conditions. To achieve breeding success, birds must continue communicating in spite of the significant decrease in the total amount of information that can be transmitted in windy situations. For the first time, to our knowledge, we have shown that a bird species takes into account the constraints imposed by wind on their acoustic communication. In windy conditions, birds try to maintain the efficiency of communication by increasing both the number of calls emitted and the number of syllables per call. This result conforms with predictions from the mathematical theory of communication: increased redundancy in a signal improves the probability of receiving a message in a noisy channel.

**Keywords:** individual recognition; penguins; communication in windy conditions

## 1. INTRODUCTION

Wind has serious consequences for sound propagation in the atmosphere. For example, wind enhances the loudness of distant sounds (Nimtz *et al.* 1992). Modification of sounds by wind can be described and predicted by different computation methods (Raspet *et al.* 1992; Nijs & Wapenaar 1992). Atmospheric conditions therefore need to be taken into account in many bio-acoustical studies. Many authors have considered the possible variation of sound due to wind, so experimental playback has often been conducted during calm weather, without wind (Weary *et al.* 1986). It has been shown that windless nights enhance the range of transmission of low-frequency sound produced by elephants (Garstang *et al.* 1998). In the same way, Henwood & Fabrick (1979) have demonstrated that at dawn signals transmit 20 times better than later on in the day. One important reason is that wind speeds are much lower at dawn than later in the day. This would partially explain why birds and primates have a peak period of communication at dawn. Nevertheless, to our knowledge, the importance of wind on acoustic communication has been poorly studied. No authors have demonstrated any change in animal behaviour to maintain the efficiency of communication in spite of windy conditions.

In the genus *Aptenodytes*, mates can recognize each other in the hubbub of the colony using only acoustic cues, via the display call (Derenne *et al.* 1979). In king penguins (*Aptenodytes patagonicus*) the two partners are faithful during at least one season and both take part in incubating and rearing the chick. Several authors (Derenne *et al.* 1979; Robisson 1993; Lengagne *et al.* 1999*a*) have described the acoustic search of the mate for nest exchange. A bird returning from the ocean (where it has been feeding) goes back to the breeding area and then calls its mate using the mutual display call. During the emission, birds hold up their head, the beak directed upwards. This calling posture improves the distance of propagation of the signal (Lengagne *et al.* 1999*b*). The partner, having fasted for several weeks on the beach, incubating the egg or rearing the chick, responds and thus gives its identity and its exact position in the colony. After a few calls, the two individuals are able to find each other and take over the egg or chick. Colonial life requires that vocal recognition occurs in the continuous background noise of the colony. Furthermore, birds breeding on the beach of sub-Antarctic islands are continuously subjected to the influence of strong circumpolar wind streams. Winds blow strongly throughout the year, generating a high level of background noise and amplitude fluctuations that may impair the communication process (Richards & Wiley 1980).

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According to the mathematical theory of communication (Shannon & Weaver 1949), the volume of information, $V$, contained in a signal can be defined by $V = FT\gamma$ (where $F$ represents frequency in hertz, $T$ signal duration in seconds and $\gamma = \log_2 (1 + S/N)$ with $S/N$ representing the signal-to-noise ratio). The channel of transmission reduces the total amount of information that can be transmitted by limiting one or several acoustic parameters. To counteract this limitation, the theory indicates a possibility that birds could use to improve the efficiency of information transfer: they maintain the volume of information by increasing the value of another parameter. In a penguin colony, the signal-to-noise ratio decreases when wind speed increases. As birds cannot increase the amplitude of their signals, since they are emitted at their maximal value (Brackenbury 1982; Gaunt *et al.* 1973), we can hypothesize that penguins increase the signal duration $T$ in order to keep constant the volume of information. Call duration can be extended in two ways: birds can extend the duration of the mutual display call or enhance the emission rate of the call when seeking a mate. To assess these possibilities, first we analysed the modification of the spectral composition of the ambient noise of the colony versus wind speed. Next, the entropy of the call was computed in two situations: with or without wind. In a third step, the call duration and the number of syllables in each call were measured in relation to different wind-speed situations. Then, the number of calls emitted by both partners was measured. Finally, we tried to assess the wind cost for the birds by measuring the total duration of the change-over in these different situations.

## 2. MATERIAL AND METHODS

### (a) *Study site and species*

The study was carried out in the summer of 1995 in Crozet Archipelago in the southern Indian Ocean (37°45′W, 46°50′S) when birds were incubating. During the reproductive season, the study colony of king penguins contained about 40 000 pairs. After a period of observation, both mates of 30 pairs were located, recorded and banded on a flipper for identification.

### (b) *Wind measurement*

To measure the wind speed, we used a Deuta anemometer (precision $\pm 0.5\ \mathrm{m\,s^{-1}}$). The wind direction was taken into account with a weather-vane set on the beach. During experiments, wind-speed measurements were noted every 5 min. In sub-Antarctic areas the wind generated by circumpolar currents blows in a regular manner without fast fluctuations during a short time period. For example, in the case of the $11\ \mathrm{m\,s^{-1}}$ wind speed used in our experiment, the mean ± s.e. value observed was $11.17 \pm 0.37\ \mathrm{m\,s^{-1}}$ ($n = 22$).

In the first group of experiments, trials were carried out either with a low wind speed, below $5\ \mathrm{m\,s^{-1}}$ (corresponding to the control condition without wind), or with an accelerated wind speed ($11\ \mathrm{m\,s^{-1}}$). For high wind-speed conditions, two situations were tested. In the first situation (downwind), the direction of the wind was favourable to the propagation of the calls, i.e. from the loudspeaker to the microphone, and in the other situation (upwind), it was opposed to the propagation of calls, i.e. from the microphone to the loudspeaker.

In the second category of experiments, calls were recorded during different wind speeds (5, 6, 7, 8, 9 and $11\ \mathrm{m\,s^{-1}}$) and with a direction opposed to the propagation.

### (c) *Recording and playback material*

The ambient noise to the colony was recorded using an omnidirectional Revox JB 10 microphone connected to a Nagra type IV tape recorder (tape speed $19\ \mathrm{cm\,s^{-1}}$, frequency range 30–20 000 Hz ± 1 dB).

Mutual display calls of king penguins were recorded with a Uher 4000C tape recorder ($19\ \mathrm{cm\,s^{-1}}$, frequency range 40–18 000 Hz ± 1.5 dB) and an omnidirectional Beyer Dynamic M69 microphone. The distance between the beak of the recorded bird and the microphone was 1 m. To avoid disturbing birds during recording sessions, the microphone was mounted on a 4 m perch. Calls used for playback studies were recorded during calm weather, without wind.

For propagation tests, display calls were broadcast with the previous tape recorder connected to a Kudelski self-powered amplifier and an Audax loudspeaker (10 W, 4Ω) and re-recorded by means of a Beyer Dynamic M69 microphone connected to the Nagra IV recorder.

Recorded taped signals were digitized with a 16 bit Oros Au21 acquisition card equipped with an anti-aliasing filter (low-pass filter, $-120\ \mathrm{dB\,octave^{-1}}$) either at a 16 kHz sample rate for the ambient noise analysis or at 12 kHz for the mutual display calls analysis.

### (d) *Spectral composition of the ambient noise*

To measure the ambient noise of the colony, two 80 s recordings were made. The recordings were made either with wind ($11\ \mathrm{m\,s^{-1}}$) or without wind. The ambient noise of the colony was examined in the spectral domain. The mean spectral composition was revealed by averaging the power of 1249 successive (overlapping 50%) fast Fourier transforms (window size of 2048 points, precision in frequency $\Delta F = 7.8$ Hz) corresponding to the analysis of the whole of each recording.

In a previous study Robisson (1991) had shown how the noise of a penguin colony is distributed in different frequency bands. In our study, we had chosen to analyse the distribution of energy through three frequency bands. The first (0–350 Hz) corresponded to physical noise, such as wind, the second (350–2000 Hz) corresponded to calls of the birds and the last (2000–8000 Hz) to the remaining noise of the colony. The distribution of energy in these frequency bands was computed using Welch's method (Oppenheim & Schafer 1989; Stearns & David 1996). Computations were done using MATLAB v. 4 and the proportion of the energy in the three frequency bands was expressed as a percentage.

### (e) *Entropy of broadcast calls*

Propagation experiments were carried out to investigate the variation of signal entropy during different wind conditions. A king penguin's call was emitted four times with an interval of 5 s silence and recorded at a distance of 8 m. This distance corresponded to the natural calling distance of an adult. Recordings were made inside the colony with a normal density of birds and consequently in a high level of background noise. Experiments were conducted in three situations: without wind, downwind and upwind.

The emergence of the penguin's signal over the background noise (colony + wind) could be measured by computing the entropy of the distribution of its energy (Shannon & Weaver 1949). If the signal emerges strongly from the background noise, it will largely modify the time distribution of the energy of the signal. On the contrary, a bird signal lost in the background noise (approximately constant over time) will not significantly modify the distribution of energy over time. The entropy $H$ was calculated according to the method described in Beecher (1988). To obtain the normalized entropy $H'$, ranging between 0 and 1, $H$ was divided by its maximum value. So, a value of $H'$ near 1 characterizes a signal almost lost in the background noise.

### (f) *Number of syllables and measurements of calls duration*

The calls of 32 incoming birds were recorded under different wind speeds as follows: six recordings for a wind speed of $5\,\mathrm{m\,s^{-1}}$, six for $6\,\mathrm{m\,s^{-1}}$, six for $7\,\mathrm{m\,s^{-1}}$, five for $8\,\mathrm{m\,s^{-1}}$, six for $9\,\mathrm{m\,s^{-1}}$ and three for $11\,\mathrm{m\,s^{-1}}$. Wind direction was opposite to that of propagation. The number of syllables and total duration of each call were measured on an envelope representation calculated by means of the analytical signal method (Mbu Nyamsi *et al.* 1993; Aubin 1994*a*).

### (g) *Duration of change-over*

Banded birds returning from the sea were located. Then, change-over between mates was analysed from the first call emitted by the incoming birds until the meeting of the two partners (i.e. with a distance of less than 0.5 m between each other). We take into account the duration corresponding to the time period between the first call emitted and the meeting. Two situations were tested: without wind for 27 pairs and with wind for ten pairs. In our specific case, for the last situation, the wind was blowing from the incoming bird to the incubating one.

### (h) *Number of calls emitted*

We measured the number of calls emitted by the banded birds returning from the sea during the acoustic search of the mate. Three situations were tested: without wind (wind speed less than $5\,\mathrm{m\,s^{-1}}$), and with upwind or downwind situations (wind speed of $11\,\mathrm{m\,s^{-1}}$). All the observations were conducted for $n=10$ change-overs between mates.

### (i) *Statistical analysis*

The fluctuation of signal normalized entropy due to the wind were represented for the three wind situations by mean ± s.e. To compare mean entropy of these situations, we used a non-parametric test (Mann–Whitney $U$-test).

We hypothesized that a piecewise linear regression could model the duration of the mutual display call and the number of syllables versus wind speed. Below a certain level of wind speed, the number of syllables as well as the duration of the call are assumed to remain constant. Above this level, when the wind begins to affect signal propagation, both tend to increase linearly with wind speed. Two separate piecewise linear models were estimated: the first relating wind speed to call duration, the second relating wind speed to the number of syllables. Both models rely on the estimation of three parameters: a wind speed threshold ($W$), a constant value for the dependent variable when wind speed is below the threshold ($K$) and the slope of the dependent variable when wind speed is above the threshold ($S$). MATLAB software was used for the estimation of models.

The non-parametric Mann–Whitney test was used to compare the number of calls emitted by the incoming bird in different windy situations. The Bonferroni-corrected $p$-values were calculated to assess the final significance of the test.

For the interval between the first call of the incoming bird and the meeting of mates, we used a linear regression. Slopes of both linear regressions were then compared.

Table 1. *Ambient noise recorded in the centre of the colony*

(The table shows the proportion of energy in three frequency bands analysed by means of the Welch calculation. Two situations were studied: with and without wind ($n=1249$ successive fast Fourier transform for each condition)).

| | energy without wind (%) | energy with wind (%) |
|---|---|---|
| frequency band 0–350 Hz (wind noise) | 9.2 | 33.0 |
| frequency band 350–2000 Hz (calls of penguins) | 59.4 | 43.0 |
| frequency band over 2000 Hz (remaining noise from the colony) | 31.4 | 24.0 |

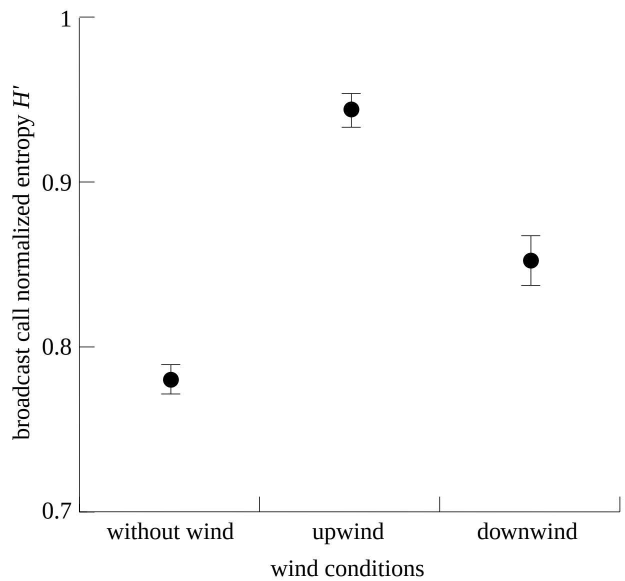


Figure 1. Normalized entropy of the bird call (mean ± s.e.) after propagation in the colony in three wind situations: without wind, with important downwind or upwind. A value near 1 characterizes a signal almost lost in the background noise ($n=4$ broadcast calls for each wind condition).

## 3. RESULTS

### (a) *Signal-to-noise ratio and amplitude fluctuation in relation to wind*

The spectra of the ambient noise of the colony and the distribution of energy in the three frequency bands were analysed in two situations: with and without wind (table 1). Compared with the situation without wind, the windy situation results in an increase of the percentage of energy in the first frequency band 0–350 Hz, in relation to the other two.

### (b) *Normalized entropy of broadcast signal*

The results indicated that values of normalized entropy were statistically significant ($p<0.01$) for situations without wind and with wind either blowing from the loudspeaker to the microphone or on the opposite side. In windy situation, values of normalized entropy of the call were greater (signal lost in background noise) than

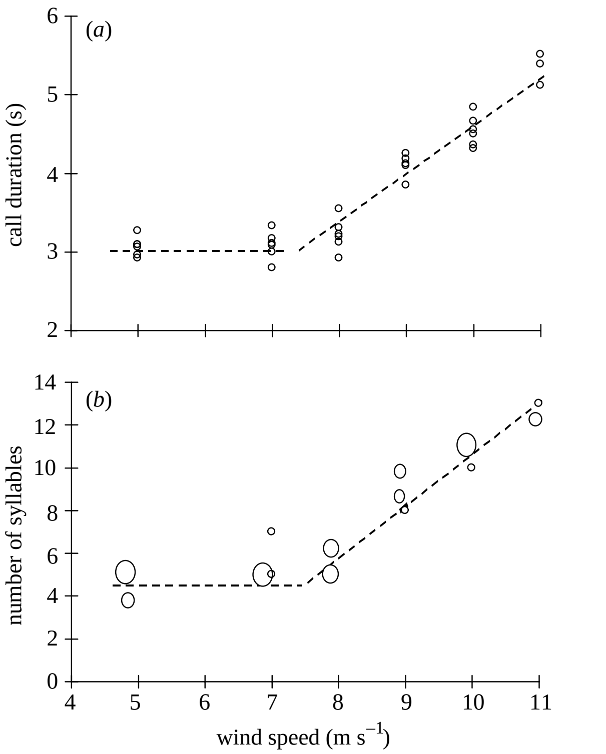


Figure 2. Importance of call parameters versus wind speed ($n = 32$). (*a*) Dashed line represents least-squares piecewise linear models relating wind speed with call duration. (*b*) Dashed line represents least-squares piecewise linear models relating wind speed with number of syllables per call. The circle size is proportional to the number of data.

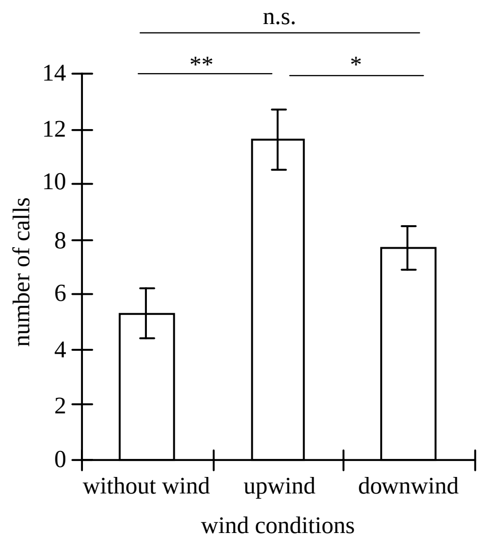


Figure 3. Number of calls emitted during the change-over in three windy conditions: without wind, upwind and downwind ($n = 10$ for each condition). The Bonferroni-corrected $p$-values were calculated to assess the final significance of the test. Significance levels: $*p < 0.05$; $**p < 0.01$.

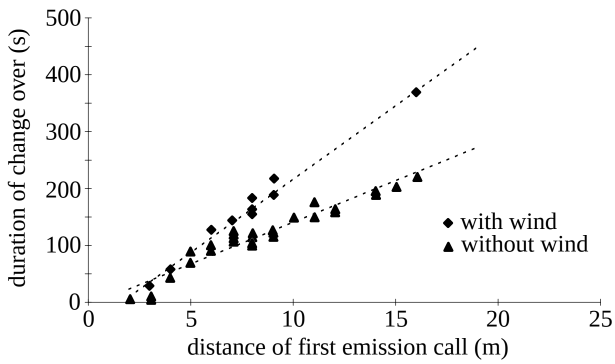


Figure 4. Duration of change-over versus wind speed. The duration corresponds to the time period between the first call emitted and the meeting of mates. Duration can be statistically represented by two regression lines (without wind $n = 27$, with wind $n = 10$).

without wind. Normalized entropy of the broadcast calls are presented in figure 1 (mean ± s.e.).

### (c) *Number of syllables and call duration*

The two separate piecewise linear models (relating wind speed to call duration and relating wind speed to the number of syllables) seem to properly fit the data (figure 2*a*,*b*). Moreover, the two separate models are in surprisingly good agreement with the values of their respective wind speed threshold, $W$. For the duration of calls, $W = 7.70\ \mathrm{m\,s^{-1}}$, for the number of syllables, $W = 7.52\ \mathrm{m\,s^{-1}}$. Below this threshold, the duration of calls is 3.07 s and the number of syllables 5.8. Above the threshold, the two models using $v$ as wind speed can be written as:

$$\text{call duration} = 0.677 \times (v - 7.70) + 3.07,$$

$$\text{number of syllables} = 1.977 \times (v - 7.52) + 5.83.$$

### (d) *Number of calls emitted*

The number of calls (mean ± s.e.) emitted by both partners during the acoustic research of the mate were computed (figure 3). In upwind condition, the number of calls emitted by the birds ($11.6 \pm 1.09$) far exceeded those measured without wind ($5.3 \pm 0.91$, $p < 0.01$) and in downwind conditions ($7.7 \pm 0.79$, $p < 0.05$). In these two later conditions, the number of calls emitted is not statistically different.

### (e) *Duration of change-over*

Results are presented in figure 4. Duration of change-over with and without wind relates linearly to the distance of first emission call. Situations can be statistically represented by two regression lines (with wind $r = 0.99$, $p < 0.001$ and without wind $r = 0.98$, $p < 0.001$).

The slopes of both regression lines were found to be statistically different ($t_{36} = 9.48$, $p < 0.01$) showing that the time necessary for change-over was more important in windy situations than without wind.

## 4. DISCUSSION

The distance over which information is transmitted is affected by the ambient noise of the environment (Wiley & Richards 1982; Aubin & Jouventin 1998; Lengagne *et al.* 1999*b*). Perception studies (Brémond 1978; Brenowitz 1982; Sorjonen 1983) showed that recognition of a signal was hampered when a continuous broad band was added, and the less the signal-to-noise ratio the more the difficulty in detecting the signal. In our study, we have shown that the level of the background noise increases in windy conditions, compared with a windless situation.

This leads to a diminution of the signal-to-noise ratio (signal designating here the entire calls emitted by the birds in the colony). In windy conditions, the emergence level of a given signal, revealed by its normalized entropy, is weak, even after a short-range propagation (8 m). This phenomenon is particularly obvious in upwind conditions: a strong wind blowing from the receiver to the emitter considerably attenuates the signal. In some cases the attenuation is so strong that the signal disappears in the background noise, even after a propagation of some metres. The king penguin call consists of a succession of broad-band sound units (syllables), each unit being separated by deep amplitude declines. These gaps of amplitude of wide-spectrum sounds facilitate the detection of a signal and result in maximal locatability (Konishi 1977). When the call of the penguin is emitted in windy conditions, the gaps of amplitude tend to disappear and consequently the detectability and the locatability of the signal are diminished.

The modality of emission of the penguin call changes as wind speed increases. From a wind speed of 8 m $s^{-1}$, the duration of the calls increases linearly as the wind speed increases. Our results show that the increase of call duration is linked to an enhancement of the number of syllables inside each call. The change is considerable since the call duration and accordingly the number of syllables in a call is multiplied by a factor of 2 with a wind speed of 11 m $s^{-1}$, compared with wind speeds below 8 m $s^{-1}$. We have also shown that the number of calls emitted by partners during the change-over period is greater in windy days than in calm days. Both these results (enhancement of the number of syllables by call and enhancement of number of calls emitted by partners before meeting) are linked to a redundancy process. By repeating the same information many times, the birds may increase the probability of communicating during a short time-window during which the wind speed suddenly drops. In previous studies (Jouventin 1982; Jouventin *et al.* 1999) we have demonstrated by playback experiments that individual recognition can be evoked whatever the choice of the syllable. So, even during calm weather, the call itself, with its succession of syllables, is redundant. This redundancy enhances the opportunity to find a quieter window in the continuous noisy environment of a sea bird colony. In windy conditions, the redundancy simply increases in a significant manner, by both a greater repetition of syllables and of calls. This result conforms with predictions from information theory that increased redundancy in signal improves the probability of receiving a message in a noisy channel (Shannon & Weaver 1949; Brémond 1978; Aubin 1994*b*). Speech intelligibility tests in psychoacoustics also show that repetition of a signal can improve recognition. When speech tokens were presented three times rather that only once in a speech-like masker, the signal-to-noise ratio necessary for recognition was reduced by between 5 and 8 dB (Fastl 1993). A theoretical model of auditory masking also predicts a considerable improvement in the detectability of signals with increasing duration, a phenomenon called temporal summation (Dooling & Searcy 1985; Klump 1996).

Repetition of an identical signal improves the receiver's performance and both the greater repetitions of calls and of syllables in upwind conditions should be seen as an acoustic adaptation. We observed an adjustment of the animal's behavioural response due to wind noise. In fact, the factors that lead to these two kinds of repetition are not the same. The repetition of calls corresponds to a passive problem of communication: the incoming bird, trying to find its partner, calls at regular intervals and at different locations in the colony. The partner calls in reply, once the signal is detected and identified, and so the meeting between the two birds occurs and the acoustic communication ceases. It seems normal that partners have to exchange a great number of calls before meeting when communication is hampered by windy conditions. In contrast, the enhancement of the number of syllables per call appears as a true acoustic adaptation to an increasing noise. It has long been assumed that the development of bird calls and songs is correlated with the physical parameters of the bird's biotope (Morton 1975; Lengagne *et al.* 1999*b*). Such adaptations are affected by a permanent condition of the environment (e.g. a forest, an open-field habitat, a colony of sea birds). The unique feature in king penguin communication is the acoustic adaptation to a temporary situation. This implies that the penguin adapts in some manner to wind speed and wind direction or noise generated by the wind or indirectly some other parameters linked to the wind by modifying the number of syllables that must be emitted. Presently, we ignore by which mechanism this correlation operates. It can only be stated that, with a strong and stable wind, the background noise is almost continuous and the quiet windows are scarce and unpredictable. Moreover, since birds increase their calling rates during windy conditions, the background noise generated by the colony slightly increases. The only noises that cover the same frequency band as that of an adult call, and which would thus lead to a strong masking effect, are precisely the calls produced by other adults (Aubin & Jouventin 1998). The emitter cannot predict when and how long it will be possible to be heard without jamming (wind and calls of other penguins in the colony). The repetition of information enhances the opportunity to find a less-noisy window and consequently to be detected.

In fact, king penguins do not fully succeed in counteracting the wind effect: the redundancy has a biological 'cost'. Repetition and other forms of sequential redundancy increase the time required for communication. In our study, we have shown that the time necessary for the change-over increased in windy situations in comparison with those without wind. As many colonial birds breeding in dense colonies, king penguins spend much time battling and pecking; this vigorous 'territorial' defence against neighbours and predators represents as many as 2500 beak pecks per 24 h (Le Maho *et al.* 1993). The more time incoming birds spend among other breeders searching for their mate in the colony, the more chances they have of getting hurt by being pecked and the more chances they have of being killed by predators, numerous in such large breeding colonies. So, by disrupting acoustic communication, wind has indirectly an influence on the breeding success of this species.

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